

New fossil birds from the earliest Eocene of Mongolia

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ABSTRACT

Understanding of the Asian early Paleogene avifauna is limited relative to that of North American and European avifauna of the same period. While major patterns of mammalian faunal exchange among these three regions across the Paleocene/Eocene boundary have been described, much less is known about the dynamics of bird diversity over the same time interval. Here, we report bird fossils from the earliest Eocene Bumban Member of the Naranbulag Formation in central Mongolia that add to the known record from Asia from just after this boundary. Most of this material, collected by the joint American Museum of Natural History/Mongolia Academy of Sciences expeditions, is referable to a previously described taxon in Presbyornithidae (Anseriformes). However, five isolated elements are identified as comprising at least four species from at least three other major avian clades. While further inclusive phylogenetic analyses of each of these clades are necessary, the new remains represent possible earliest occurrences in Asia of these clades. The material includes a humerus and a furcula from shorebirds (Pan-Charadriiformes), a quadrate from a stem member of the flamingo-grebe lineage (Pan-Mirandornithes), and a coracoid from a stem galliform (Pangalliformes). We also report a humerus with uncertain phylogenetic affinities but with similarities to core Gruiformes. These new fossils expand our knowledge of the Asian avifauna during this time and have the potential to further inform our understanding of the early biogeography of these clades. The shorebird and flamingo-grebe material indicate that both these lineages were present in Asia by the earliest Eocene. The pan-mirandornithine quadrate provides insight into the early feeding ecology of the flamingo-grebe clade.

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INTRODUCTION

The mammalian fossil record of Asia during the earliest Eocene is relatively well characterized and marks a major period of faunal turnover, including the first appearances on the continent of primates, perissodactyls, and artiodactyls (Dashzeveg, 1988; Meng and McKenna, 1998; Bowen et al., 2002; Kondrashov et al., 2004; Smith et al., 2006; Bajpai et al., 2008). By contrast, the Asian avifauna from this interval remains poorly understood, and bird remains from key mammal-bearing deposits are poorly sampled (Mayr, 2009; Hwang et al., 2010). In Asia, only nine bird taxa are currently described from the Paleocene and at least 33 from the Eocene (table 1). Many of these taxa are described from fragmentary single elements.

The Eocene Naranbulag Formation of Mongolia holds potential to inform our understanding of avian diversity at this time. Naranbulag Formation fossils have greatly contributed to our understanding of early Paleogene mammal diversity in Asia (Dashzeveg et al., 1998, and citations therein). The lower bound of the Bumban Member of this formation is placed at or just after the Paleocene-Eocene boundary based on biostratigraphic correlation of the Bumban fauna with other faunal assemblages (Dashzeveg, 1988; Meng and McKenna, 1998; Bowen et al., 2002), and was constrained to between 55.7–54.97 Ma by Bowen et al. (2002) using isotope stratigraphy, magnetostratigraphy, and quantitative biochronology. Several fossiliferous mammalian sites are located in the Bumban Member, including the Tsagaan Khushuu “Quarry 1” locality described by Dashzeveg et al. (1998: 194) as containing, “one of the most diverse early Eocene faunas known from Asia.” Avian remains from the Naranbulag Formation are comparatively rare. The Bumban Member has produced abundant isolated elements of the extinct anseriform *Presbyornis* (Kurochkin and Dyke, 2010), as well as isolated records of proposed stem owls (Strigiformes [Kurochkin and Dyke, 2011]) and the earliest Asian record of a stem-member landfowl (Pangalliformes [Hwang et al., 2010]).

Here, we report new avian remains recovered from the Bumban Member by joint American Museum of Natural History/Mongolia Academy of Sciences expeditions between 2000 and 2002. All material was recovered from in and around “Quarry 2” of Dashzeveg et al. (1998) at Tsagaan Khushuu in the Nemegt Basin, Mongolia (fig. 1). This site lies at the base of the Bumban Member, suggesting an age of ~55 Ma. Out of the 86 collected avian elements, ~20% (19 specimens) are readily identifiable as presbyornithid remains, and much of the rest is fragmentary and nondiagnostic. Five of the remaining specimens can be unambiguously distinguished from presbyornithids. Of these, three represent proposed earliest records of their respective lineages in Asia.

MATERIALS AND METHODS

Quadrates terminology follows Elzanowski and Stidham (2010). All other osteological terminology follows Baumel and Witmer (1993). All terms have been anglicized. All measurements are in mm. IGM 100/1268 and IGM 100/1418 were scanned using high-resolution 3D X-ray computed tomography (CT) at the University of Texas High-Resolution X-ray Computed Tomography Facility, Austin, Texas (UTCT) on 22–23 May 2018, on a NSI scanner with a Fein Focus

Table 1. A summary of the Paleogene fossil bird record of Asia. Also see earlier reviews in Nesson (1992), Mayr (2009) and Wang et al. (2012a).

Species	Clade	Age	Locality	Reference
<i>Qinornis paleocenica</i> *	Ornithurae	Early Paleocene	China	Xue, 1995
<i>Protoplotus beauforti</i>	Protoplotidae, Suliformes	Paleocene	Sumatra	Lambrecht, 1931; van Tets et al., 1989; Stidham et al., 2005
<i>Wanshuina lii</i>	?Rallidae, 'Gruiformes'	Paleocene	China	Hou, 1994
<i>Qianshanornis rapax</i>	Qianshanornithidae	Middle Paleocene	China	Mayr et al., 2013a
<i>Nanbulagornis khun</i>	Anseriformes	Late Paleocene	Mongolia	Zelenkov, 2019
<i>Odontopteryx "Pseudontornis" tsulensis</i>	Pelagornithidae, Odontopterygiformes	Late Paleocene	Kazakhstan	Averianov et al., 1991
<i>Eopuffinus kazakhstanensis</i>	Procellariiformes	Late Paleocene	Kazakhstan	Nesson, 1986
<i>Tshulia litorea</i> **	Prophaethontidae, Phaethontiformes	Late Paleocene	Kazakhstan	Nesson, 1988; Mayr and Scofield, 2016
<i>Zhylgaia aestiflua</i>	Prophaethontidae, Phaethontiformes	Late Paleocene	Kazakhstan	Nesson, 1988; Bourdon et al., 2008; Mayr and Scofield 2015
? <i>Berruornis</i> sp.	Strigiformes	Late Paleocene	Kazakhstan	Nesson, 1992
Unnamed	Galliformes	Early Eocene	Mongolia	Hwang et al., 2010
" <i>Zhongyuanus</i> "	Gastornithidae, Anseriformes	Early Eocene	China	Hou, 1980; Buffetaut, 2013
<i>Gastornis xichuanensis</i>				
<i>Songzia heidangkouensis</i>	'Gruiformes'	Early Eocene	China	Hou, 1990; Wang et al., 2012a
Unnamed	Indet.	Early Eocene	Mongolia	
1 or 2 Unnamed	Pan-Charadriiformes	Early Eocene	Mongolia	
Unnamed	Pan-Mirandornithes	Early Eocene	Mongolia	
Unnamed	?Quercymegapodiidae, Pangalliformes	Early Eocene	Mongolia	
<i>Presbyornis mongoliensis</i>	Presbyornithidae, Anseriformes	Early Eocene	Mongolia	Kurochkin and Dyke, 2010
<i>Presbyornis</i> sp. indet.	Presbyornithidae, Anseriformes	Early Eocene	Mongolia	Kurochkin and Dyke, 2010
<i>Eostrix tsaganica</i>	Protostrigidae, Strigiformes	Early Eocene	Mongolia	Kurochkin and Dyke, 2011
<i>Romainvillia kazakhstanensis</i>	Romainvillidae, Anseriformes	Early Eocene	Kazakhstan	Zelenkov, 2018
Unnamed	cathartid-like	Early Eocene	India	Mayr et al., 2010

Table 1. Continued

Species	Clade	Age	Locality	Reference
Unnamed	Indet.	Early Eocene	India	Mayr et al., 2013b
<i>Vastanavis cambayensis</i>	Vastanavidae, ?Psittaciformes	Early Eocene	India	Mayr et al., 2010
<i>Vastanavis eocaena</i>	Vastanavidae, ?Psittaciformes	Early Eocene	India	Mayr et al., 2007; Mayr et al., 2010
<i>Vastanavis</i> sp.	Vastanavidae, ?Psittaciformes	Early Eocene	India	Mayr et al., 2010
<i>Jiliniornis huadianensis</i>	?Charadriidae, Charadriiformes	Middle Eocene	China	Hou and Ericson, 2002
<i>Eociconia sangequanensis</i>	Ciconiidae, Ciconiiformes	Middle Eocene	China	Hou, 1989
<i>Sanshuicornis zhangii</i>	?Ciconiiformes	Middle Eocene	China	Wang et al., 2012b
Unnamed	galliform-like	Middle Eocene	Ukraine	Mayr and Zvonok, 2011
<i>Colymbiculus udovichenkoi</i>	Gaviidae, Gaviiformes	Middle Eocene	Ukraine	Mayr and Zvonok, 2011
Unnamed	gruiform-like	Middle Eocene	Ukraine	Mayr and Zvonok, 2011
<i>Dasornis</i> sp.	Pelagornithidae, Odontopterygiformes	Middle Eocene	Ukraine	Mayr and Zvonok, 2011
<i>Lutetodontopteryx tethyensis</i>	Pelagornithidae, Odontopterygiformes	Middle Eocene	Ukraine	Mayr and Zvonok, 2012
<i>Kievornis rogovitshi</i>	?Procellariiformes	Middle Eocene	Ukraine	Averianov et al. 1990; Zvonok et al., 2015
<i>Mangystania humilicristata</i>	?Suliformes	Middle Eocene	Kazakhstan	Zvonok et al., 2016
<i>Murunkus subitius</i>	?Procellariiformes	Middle Eocene	Uzbekistan	Panteleyev and Nesson, 1993
Unnamed	?Threskiornithidae, Ciconiiformes	Middle Eocene	Myanmar	Stidham et al., 2005
<i>Xorazmoryx turkestanensis</i>	Paraortygidae, Galliformes	Middle Eocene	Uzbekistan	Zelenkov and Panteleyev, in press
<i>Zheroia kurochkini</i>	'Gruiformes'	Middle Eocene	Uzbekistan	Nesson, 1988
<i>Eogrus aeola</i>	Eogruidae, Gruiformes	Mid-Late Eocene	Kazakhstan, Mongolia	Wetmore, 1934
2 Unnamed	Anatidae, ?Romainvilliinae, Anseriformes	Late Eocene	China	Stidham and Ni, 2014
<i>Eogrus crudus</i>	Eogruidae, Gruiformes	Late Eocene	Mongolia	Kurochkin, 1981
<i>Eogrus turanicus</i>	Eogruidae, Gruiformes	Late Eocene	Kazakhstan	Kurochkin, 1981; Bendukidze 1971
<i>Telecrex grangeri</i>	?Phasianidae, Galliformes	Late Eocene	Mongolia	Wetmore, 1934; Olson, 1974
<i>Minggangia changgouensis</i>	Threskiornithidae, Ciconiiformes	Late Eocene	China	Hou, 1982
<i>Cygnavus formosus</i>	Anatidae, Anseriformes	Early Oligocene	Kazakhstan	Kurochkin, 1968

Table 1. Continued

Species	Clade	Age	Locality	Reference
<i>Ergilornis rapidus</i>	Eogruidae, Gruiformes	Early Oligocene	Mongolia	Kozlova, 1960
<i>Ergilornis minor</i>	Eogruidae, Gruiformes	Early Oligocene	Mongolia	Kozlova, 1960
<i>Sonognus gregalis</i>	Eogruidae, Gruiformes	Early Oligocene	Mongolia	Kurochkin, 1981
<i>Heterostrix tatsinensis</i>	Heterostriidae, Strigiformes	Early Oligocene	Mongolia	Kurochkin and Dyke, 2011
<i>Buteo circoides</i>	Accipitridae, Accipitriformes	Oligocene	Mongolia	Kurochkin, 1968
<i>Venerator dementjevi</i>	Accipitridae, Accipitriformes	Oligocene	Mongolia	Kurochkin, 1968
<i>Gobinierax edax</i>	Accipitridae, Accipitriformes	Oligocene	Mongolia	Kurochkin, 1968
? <i>Somateria</i> sp.	Anatidae, Anseriformes	Late Oligocene	Kazakhstan	Kurochkin, 1968
<i>Colymboides</i> sp.	Gaviiformes	Late Oligocene	Kazakhstan	Kurochkin, 1976
<i>Palaeorallus alienus</i>	Galliformes	Oligocene	Mongolia	Kurochkin, 1968; Cracraft, 1973
<i>Limicorallus saienis</i>	Phalacrocoracidae, Suliformes	Late Oligocene	Kazakhstan	Kurochkin, 1968
<i>Cygnopterus lambrechtii</i>	Phoenicopteriformes	Late Oligocene	Kazakhstan	Kurochkin, 1968; Zelenkov, 2013
<i>Agnopterus turgaiensis</i>	Phoenicopteridae, Phoenicopteriformes	Late Oligocene	Kazakhstan	Tugarinov, 1940; Mlikovsky and Svec, 1986; Zelenkov, 2013
Unnamed	Plotopteridae, Suliformes	Oligocene	Japan	Hasegawa et al., 1979
<i>Copepteryx hexeris</i>	Plotopteridae, Suliformes	Late Oligocene	Japan	Olson and Hasegawa, 1996
<i>Copepteryx titan</i>	Plotopteridae, Suliformes	Late Oligocene	Japan	Olson and Hasegawa, 1996
<i>Hokkaidornis abashiriensis</i>	Plotopteridae, Suliformes	Late Oligocene	Japan	Sakurai et al., 2008
<i>Megagallinula harundinea</i>	?Rallidae, Gruiformes	Late Oligocene	Kazakhstan	Kurochkin, 1968

**Qinornis paleocenica* is likely a non-neornithine (Xue, 1995).

** *Tshulta litorea* is proposed to be a synonym of *Zhylgata aestiflua* by Mayr and Scofield (2015).



FIGURE 1. Map showing the location of Tsagaan Khushuu locality in the central Gobi Desert of Mongolia, where the fossils were recovered (modified from Clarke and Norell, 2004).

Microfocal X-ray source. IGM 100/1268 was scanned at 130 kV/0.14 mA with voxel size = 15.6 μm , resulting in 1981 total slices. IGM 100/1418 was scanned at 130 kV/0.14 mA with voxel size = 9.7 μm , resulting in 983 total slices. Data was visualized and segmented in Avizo 9.3 (FEI).

INSTITUTIONAL ABBREVIATIONS: **IGM**, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **GPIM**, Institute of Geosciences of Johannes-Gutenberg-University Mainz, Germany; **TMM**, Texas Memorial Museum, Austin, Texas; **USTL**, Laboratoire de Paléontologie de l'Université des Sciences et Techniques du Languedoc, Montpellier, France.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

PAN-CHARADRIIFORMES, new clade

DEFINITION: "Pan-Charadriiformes" refers to the clade containing all birds more closely related to *Charadrius hiaticula* and *Sterna hirundo* than to flamingos and grebes (Mirandornithes) based on the Prum et al. (2015) reference phylogeny.

Gen. et sp. indet.

Figure 2

REFERRED SPECIMEN: IGM 100/1435 (distal end of left humerus; fig. 2).

MEASUREMENTS: Dorsoventral width of distal end, 4.7 mm.

REMARKS: IGM 100/1435 is broken immediately proximal to the dorsal supracondylar process. This humerus is from a bird slightly smaller than the smallest extant sandpiper, *Calidris minutilla* (Least Sandpiper). The fossil exhibits a well-developed dorsal supracondylar process, which projects from the shaft well proximal to the dorsal condyle. The tip is rounded and is directed proximally, and it has a slight sigmoidal curve along the base of its dorsal margin. The fossa for the m. brachialis is preserved as a shallow scar with a well-demarcated ventral

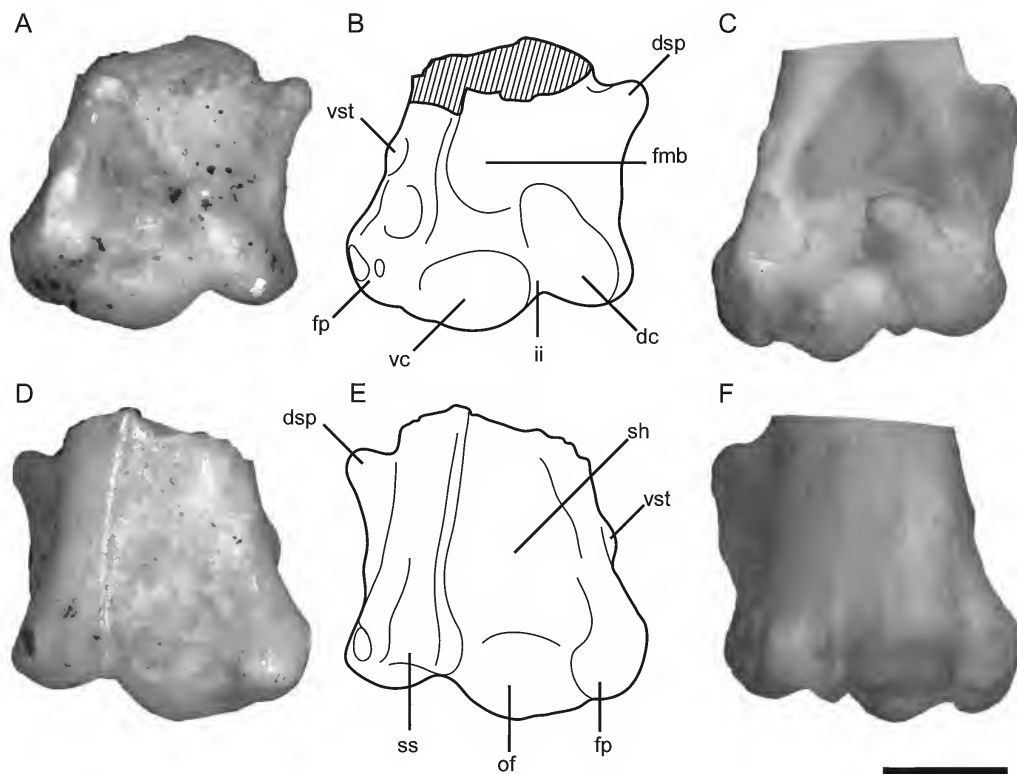


FIGURE 2. Photographs and line drawings of the left distal humerus of a fossil shorebird specimen, IGM 100/1435, in **A** and **B**, cranial; and **D** and **E**, caudal views, compared to the left distal humerus of a Western Sandpiper *Calidris mauri* (TMM M-2742) in **C**, cranial; and **F**, caudal views. Abbreviations: **dc**, dorsal condyle; **dsp**, dorsal supracondylar process; **fp**, flexor process; **ii**, intercondylar incisure; **fmb**, fossa for the m. brachialis; **of**, olecranon fossa; **sh**, sulcus for the m. humerotricipitalis; **ss**, sulcus for the m. scapulotricipitalis; **vc**, ventral condyle; **vst**, ventral supracondylar tubercle. Scale bar = 2 mm.

terminus and fainter margins proximally and dorsally (fig. 2A, B). The dorsal and ventral condyles are of similar maximum length (fig. 2A, B, D, E), and the flexor process is short and broad. The olecranon fossa is deep and undercuts the edge of the flexor process, giving that process a dorsally hooked margin in caudal view. A ridge separates the sulcus for the m. scapulotricipitalis from the sulcus for the m. humerotricipitalis. The sulcus for the m. scapulotricipitalis is narrower than the sulcus for the m. humerotricipitalis (fig. 2D, E).

COMPARISONS: A well-developed dorsal supracondylar process as in IGM 100/1435 is observed in shorebirds, tubenoses (Procellariiformes), swifts and hummingbirds (Apodiformes), and songbirds (Passeriformes) among extant birds. However, the new fossil humerus is otherwise dissimilar in size and proportion to those found in swifts, hummingbirds, and songbirds; specifically, the dorsal supracondylar process is more strongly projected as well as being angled more cranially than dorsally. In the new fossil, this process is narrow and projects proximally, consistent with shorebirds (fig. 2C); by contrast, in tubenoses this process is broad and projects more cranially (Hou and Ericson, 2002). Additionally, this fossil shows a distinct

sulcus for the *m. scapulotricipitalis*, which is observed in shorebirds but not in tubenoses (Zvonok et al., 2015). The new fossil can be further differentiated from most tubenoses by the presence of a shallow fossa for the *m. brachialis*; among nonalbatross tubenoses, this fossa is deep. IGM 100/1435 also exhibits a ventral condyle that projects distally past the dorsal condyle, consistent with shorebirds but not tubenoses, in which these two condyles show similar distal projections (Zvonok et al., 2015). Features of the distal humerus alone are not diagnostic for most lineages within shorebirds (Zvonok et al., 2015; Mayr, 2016), so further taxonomic assignment for the new specimen is not possible. Because this fossil cannot be assigned to crown-group charadriiforms, we place this new fossil within Pan-Charadriiformes.

A slightly younger (~2–3 Ma) distal humerus (SMF Av 619) was reported from the early Eocene Nanjemoy Formation of Virginia (Mayr, 2016). This specimen is similar in size to IGM 100/1435 but has a shallower fossa for the *m. brachialis* and the dorsal supracondylar process has a slightly narrower base.

Gen. et sp. indet.

Figure 3

REFERRED SPECIMEN: IGM 100/1268 (furcula missing both omal extremities; fig. 3).

MEASUREMENTS: Maximum preserved length of right ramus, 13.7 mm; maximum length of furcular apophysis, 3 mm; maximum preserved interclavicular width from lateral margins of rami, 7.5 mm.

REMARKS: The apophysis of IGM 100/1268 is slightly crushed but retains its shape in lateral view. Mechanical preparation of the fragile rami and apophysis is impossible, and so these parts of the specimen remain encased in rock. Digitally “prepped” renderings derived from high-resolution CT data were used for comparison with other birds. The fossil is from an individual slightly smaller than the extant Least Sandpiper. The furcula is a narrow U-shape in cranial view. Toward the apophysis, the rami mediolaterally broaden and dorsoventrally flatten (fig. 3A, C). The furcular apophysis is bladelike and sharply projects dorsally and perpendicularly to the rami (fig. 3A). The ventral margin is curved in lateral view (fig. 3A).

COMPARISONS: IGM 100/1268 has a well-developed, bladelike furcular apophysis, similar to those of charadriiforms, passeriforms, and galliforms (e.g., Fürbringer, 1888; Nesbitt et al., 2009; Smith, 2014). Among these groups, the new fossil is most similar to small extant charadriiforms (e.g., *Calidris*, *Charadrius*, *Turnix*), which also exhibit furculae with dorsally directed apophyses as well as dorsoventrally compressed and gently ventrally curved rami (Smith, 2014; fig. 3B, D). By contrast, the apophysis in galliforms is elongate and projects sternodorsally, well past the sternal margin of the rami, resulting in more V-shaped furculae (Fürbringer, 1888; Nesbitt et al., 2009). Galliforms also do not exhibit the curvature of the rami observed in IGM 100/1268 in lateral view. Passeriforms have furculae with rami that are variably arched or curved in lateral view and are highly dorsoventrally compressed, with no appreciable broadening toward the sternal extremity, unlike in IGM 100/1268. Based on these comparisons we assign IGM 100/1268 to Pan-Charadriiformes.

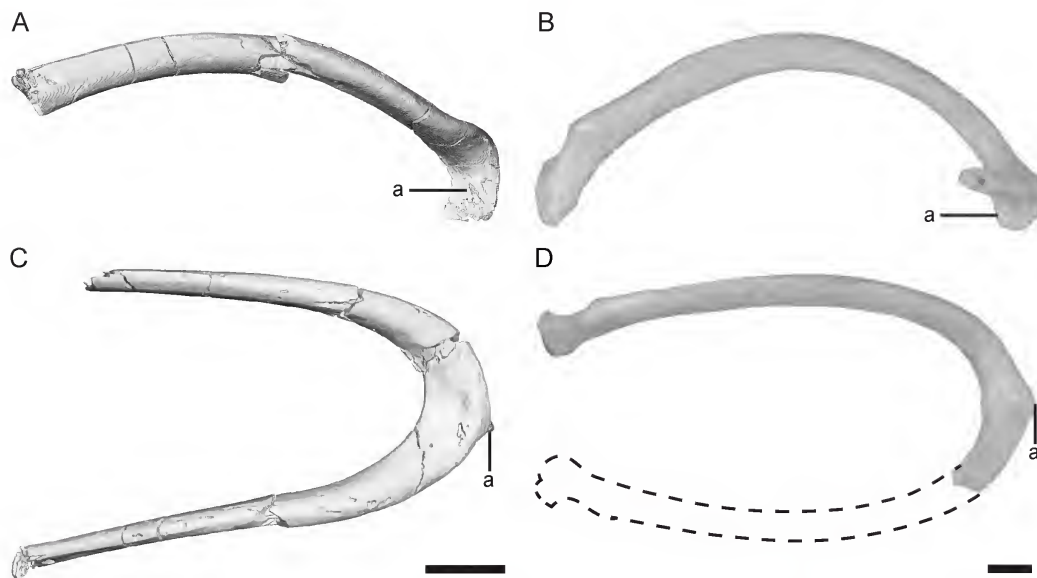


FIGURE 3. Digital renderings from CT data of the furcula of a second fossil shorebird specimen, IGM 100/1268, in **A**, right lateral, and **C**, dorsal views, compared to the furcula of a Killdeer *Charadrius vociferous* (TMM M-3245) in **B**, right lateral, and **D**, dorsal views. Abbreviation: a, furcular apophysis. Scale bars = 2 mm.

PAN-MIRANDORNITHES, new clade

DEFINITION: “Pan-Mirandornithes” refers to the clade including all birds more closely related to *Phoenicopterus ruber* and *Podiceps cristatus* than to shorebirds (Charadriiformes) based on the reference phylogeny in Prum et al. (2015).

REFERRED TAXA: In addition to crown-group Mirandornithes (flamingos and grebes), Pan-Mirandornithes also includes the proposed stem mirandornithine *Juncitarsus* (Olson and Feduccia, 1980; Mayr, 2014).

Gen. et sp. indet.

Figure 4

REFERRED SPECIMEN: IGM 100/1418 (left quadrate lacking most of the orbital process).

MEASUREMENTS: Lateromedial width of mandibular articulation, 6 mm; maximum dorso-ventral height, 9.4 mm.

REMARKS: IGM 100/1418 shows slight abrasion of the otic process and body. It is similar in size to the quadrate of the extant grebe *Podiceps grisegena* (Red-Necked Grebe). We used digital renderings derived from high-resolution CT scan data to aid comparison with other taxa.

The otic and squamosal facets are both slightly abraded, and the intercapitular incisure is wide and shallow (fig. 4A, B, K, L). A distinct tympanic crest runs ventromedially from the lateral margin of the squamosal facet to the medial face of the body where it meets the medial crest (fig. 4A, B, E,

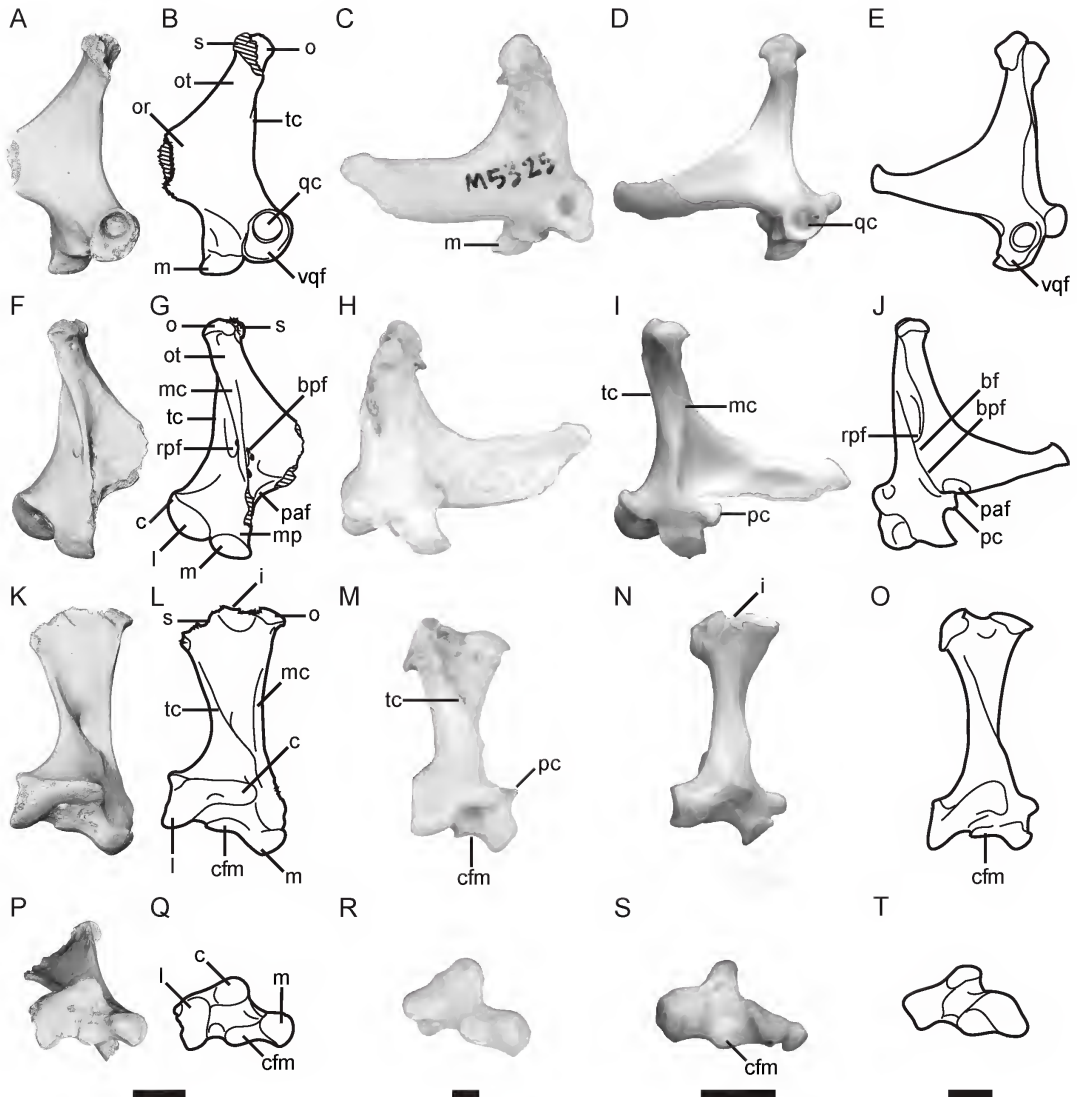


FIGURE 4. Comparison of the left quadrates of Pan-Mirandornithes, including digital rendering from CT data and line drawings of the proposed Mongolian pan-mirandornithine, IGM 100/1418, in **A**, **B**, lateral; **E**, **G**, medial; **K**, **L**, caudal; and **P**, **Q**, ventral views; Chilean Flamingo *Phoenicopterus chilensis* (TMM M-5325) in **C**, lateral; **H**, medial; **M**, caudal; and **R**, ventral views; Eared Grebe *Podiceps nigricollis* (TMM M-1394) in **D**, lateral; **I**, medial; **N**, caudal; and **S**, ventral views; and line drawings of *Palaelodus ambiguus* (GPIM Op 395) based on photographs in Mayr (2015) in **E**, lateral; **J**, medial; **O**, caudal, and **T**, ventral views. Abbreviations: **bf**, basiorbital fossa; **bpf**, basiorbital pneumatic foramina; **c**, caudal condyle; **cfm**, convex articular facet of medial condyle; **i**, intercapitular incisure; **l**, lateral condyle; **m**, medial condyle; **mc**, medial crest; **mp**, medial process; **o**, otic facet; **or**, orbital process; **ot**, otic process; **paf**, pterygoid articular facet; **pc**, pterygoid condyle; **qc**, quadratojugal cotyle; **rpf**, rostromedial pneumatic foramina; **s**, squamosal facet; **tc**, tympanic crest; **vqf**, ventral quadratojugal facet. Scale bars = 2 mm.

G, L, K). The medial crest is also well defined and runs from the medial margin of the otic facet down to the medial condyle (fig. 4F, G). Between these crests lies a deep furrow, containing four small dorsoventrally aligned pneumatic foramina (fig. 3B). The basiorbital fossa, bounded by the medial crest and the base of the orbital process, contains three additional basiorbital pneumatic foramina also arranged in a line (fig. 4F, G). No caudomedial pneumatic foramina are present.

The pterygoid articulation is conformed as a facet on the medial base of the orbital process (fig. 4F, G). The specimen lacks a pterygoid condyle on the medial process, but it is unclear whether it is missing due to breakage (fig. 4F, G, K, L). The mandibular articulation consists of distinct lateral, caudal, and medial condyles. The medial condyle is convex mediorostrally with a small lip and is developed laterally as a concave articular facet (fig. 4K, L, P, Q). The lateral and caudal condyles are nearly confluent, separated by a shallow depression (fig. 4K, L, P, Q). The lateral process is moderately projected and bears a deeply concave quadratojugal cotyle with a complete, rounded margin (fig. 4A, B). The ventral margin of this cotyle is markedly expanded into a rostroventrally oriented lip in lateral view (fig. 4A, B, K, L).

COMPARISONS: We assign IMG 100/1418 to *Pan-Mirandornithes* based on the following suite of characters: a wide and shallow intercapitular incisure; a gracile quadrate body; a deep furrow bounded by the tympanic and medial crests; a concave articular facet lateral of the medial condyle; a rostrally projecting lip formed by the medial condyle; and a deeply concave quadratojugal socket. The combined presence of rostromedial and basiorbital pneumatic foramina is observed in both extant and stem flamingos (e.g., *Palaelodus*). These foramina are absent in most grebes (fig. 4I); however, a loss of pneumatic foramina is commonly observed in diving birds (Witmer, 1990; Mayr, 2015). This same combination of foramina placement has otherwise been reported only in some gulls (*Laridae*; Samejima and Otsuka, 1987; Mayr, 2015). However, in gulls, these foramina are relatively much larger than those observed in the new fossil and in stem and crown flamingos.

IMG 100/1418 exhibits additional similarities with the much younger (by ~20 Ma) stem flamingo *Palaelodus ambiguus* (Milne-Edwards, 1863; Cheneval and Escuillie, 1992), known from the Oligo-Miocene of Europe, which are not observed in extant flamingos and grebes. These characters include a distinct furrow bounded by the medial crest and the base of the orbital process (fig. 4J), as well as a pterygoid articular facet located on the medial base of the orbital process (Mayr, 2015; fig. 4J). It differs from *Palaelodus* by exhibiting a concave caudal margin in lateral and medial views, whereas in *Palaelodus* this margin is straight (fig. 4E, J). *Palaelodus* also has a more ventrally projecting lip on the quadratojugal facet (fig. 4E) and a more rostrally projecting lip on the medial condyle (fig. 4J) than in the new fossil. The new fossil can be differentiated from *Presbyornis* spp., the most abundant avian taxon from this locality, by its trituberculate mandibular articulation (presence of a caudal condyle). In contrast, *Presbyornithidae* bears only two mandibular condyles (lateral and medial), consistent with other galloanserines (e.g., Cracraft and Clarke, 2001; Mayr and Clarke, 2003). The isolated nature of the new fossil and the lack of relevant comparative material available for other proposed pan-mirandornithines outside the crown group (e.g., *Juncitarsus*; Olson and Feduccia, 1980; Peters, 1987; Mayr, 2014) prevent a confident taxonomic assignment within *Mirandornithes*.

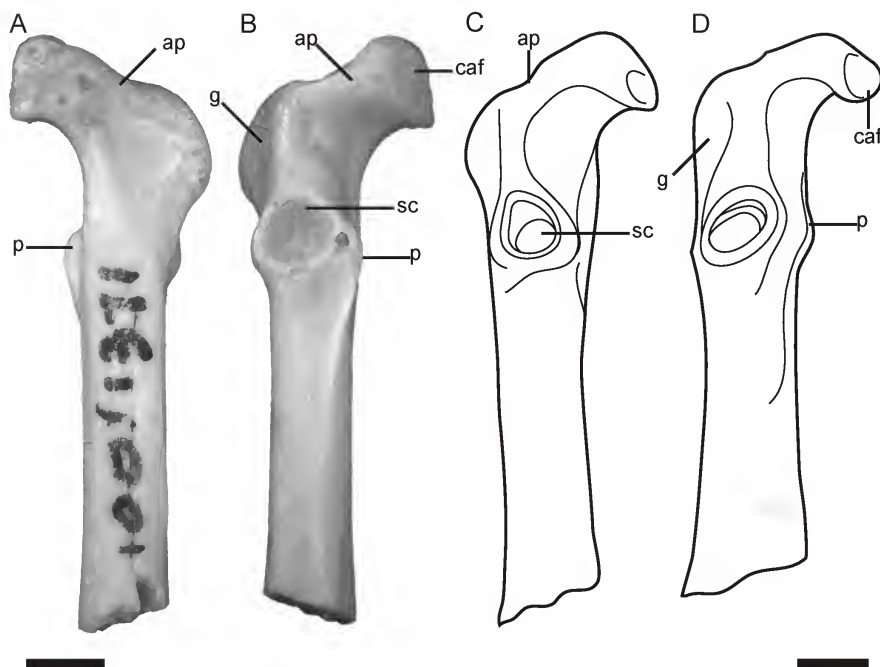


FIGURE 5. Comparison of the omal ends of the coracoids of Pangalliformes, including the new fossil, IGM 100/1371, in **A**, ventral; and **B**, dorsal views; line drawings of **C**, *Quercymegapodius depereti* (USTL SNB 700) (Quercymegapodiidae); and **D**, *Paraortyx lorteti* (USTL MGB 1547) (Paraortygidae), in dorsal view, based on photographs in Mourer-Chauviré (1992). Abbreviations: **ap**, acrocoracoid process; **caf**, clavicular articular face; **g**, glenoid facet; **p**, procoracoid; **sc**, scapular cotyla. Scale bars = 2 mm.

PANGALLIFORMES Clarke, 2002

cf. QUERCYMEGAPODIIDAE Mourer-Chauviré, 1992

Gen. et sp. indet.

Figure 5

REFERRED SPECIMEN: IGM 100/1371 (omal end of left coracoid).

MEASUREMENTS: Maximum length as preserved, 13.6 mm; maximum mediolateral width of omal end, 4.7 mm.

REMARKS: The dimensions of IGM 100/1371 indicate that it is from a bird significantly smaller than the smallest extant galliform, *Excalfactoria chinensis* (King Quail). The shaft is narrow with negligible sternal expansion. It bears a deeply concave scapular cotyle with a rounded, slightly teardrop shape (fig. 4B). There is no foramen associated with the passage of the n. supracoracoideus. The acrocoracoid process is hooked with its lip forming a near-perpendicular ($\sim 100^\circ$) angle to the shaft (fig. A, B). The clavicular articular face is flat. The well-projected glenoid facet terminates at the omal margin of the scapular cotyla (fig. 5B). The procoracoid process is reduced, appearing only as a slight ridge along the medial margin mediosternal to the scapular cotyla (fig. 5B).

COMPARISONS: The morphology of IGM 100/1371 is consistent with Galliformes in its narrow shaft, hooked acrocoracoid, greatly reduced procoracoid process, and lack of a supracondylar nerve foramen. A concave scapular cotyle like that of the new fossil is not observed among crown-group galliforms but is present in stem members of the clade and considered the ancestral condition in birds (Mayr, 2000; Clarke, 2002, Mayr and Weidig, 2004). Based on these traits we assign IGM 100/1371 to the clade Pangalliformes.

Among stem galliforms, the coracoid is most like the middle-late Eocene Quercymegapodiidae with respect to the subcircular scapular cotyle, parallel medial and lateral margins of the shaft, and a near-perpendicular angle formed by the hooked acrocoracoid and the shaft. By contrast, other stem galliforms (e.g., the early Eocene Gallinuloididae and the middle-late Eocene Paraortygidae) exhibit more mediolaterally broad scapular cotylae, sternally diverging lateral and medial margins of the midshaft, and more obtuse acrocoracoid-to-shaft angles (Mourer-Chauviré, 1992; Mayr, 2000, 2006; Mayr, and Weidig, 2004; fig. 5D). The new specimen can be differentiated from previously reported Quercymegapodiidae by its subplanar clavicular articular face, which in other quercymegapodiids is slightly concave (e.g., *Quercymegapodius*; fig. 5C) or convex (e.g., *Ameripodius*) (Mourer-Chauviré, 1992, Mourer-Chauviré, 2000). The acrocoracoid process is also more hooked in IGM 1371 than in these taxa or in *Taubacrex* (Alvarenga, 1988; Mourer-Chauviré, 1992, Mourer-Chauviré, 2000).

Aves, gen. et sp. indet.

Figure 6

REFERRED SPECIMEN: IGM 100/1360 (distal end of left humerus).

MEASUREMENTS: Dorsoventral width of distal end, 5 mm.

REMARKS: IGM 100/1360 is broken proximal to the dorsal supracondylar tubercle. It is from a bird slightly larger than *Porzana carolina* (Sora Rail). The dorsal supracondylar tubercle is a proximodistally elongate rectangular projection with a slight depression on its dorsal margin (fig. 6A, B). The fossa for the m. brachialis is elongate and ventrally positioned, with clearly demarcated ventral and distal edges (fig. 6A, B). Both the ventral and dorsal condyles are weakly cranially projected. The ventral condyle is roughly half the length of the dorsal condyle and extends distal to the dorsal condyle (fig. 6A, B). The flexor process is similar in distal extent to the dorsal condyle (fig. 6A, B, D, E). Both the m. scapulotricipitalis sulcus and the olecranon fossa are broad and shallow (fig. 6D, E).

COMPARISONS: IGM 100/1360 exhibits a combination of conditions consistent with a position within the clade Messelornithidae + Ralloideae (rails and allies) (Mayr, 2004), including: craniocaudal compression, a proximodistally elongate dorsal supracondylar tubercle bearing a concavity on its margin, a narrow and ventrally situated fossa for the m. brachialis, and a well-developed flexor process (fig. 6C, F). These characters can be observed in several fossil and extant taxa of this group; the Paleocene “messel rail” *Walbeckornis creber* (Messelornithidae), the early Oligocene *Bellgirallus* (Rallidae), the early

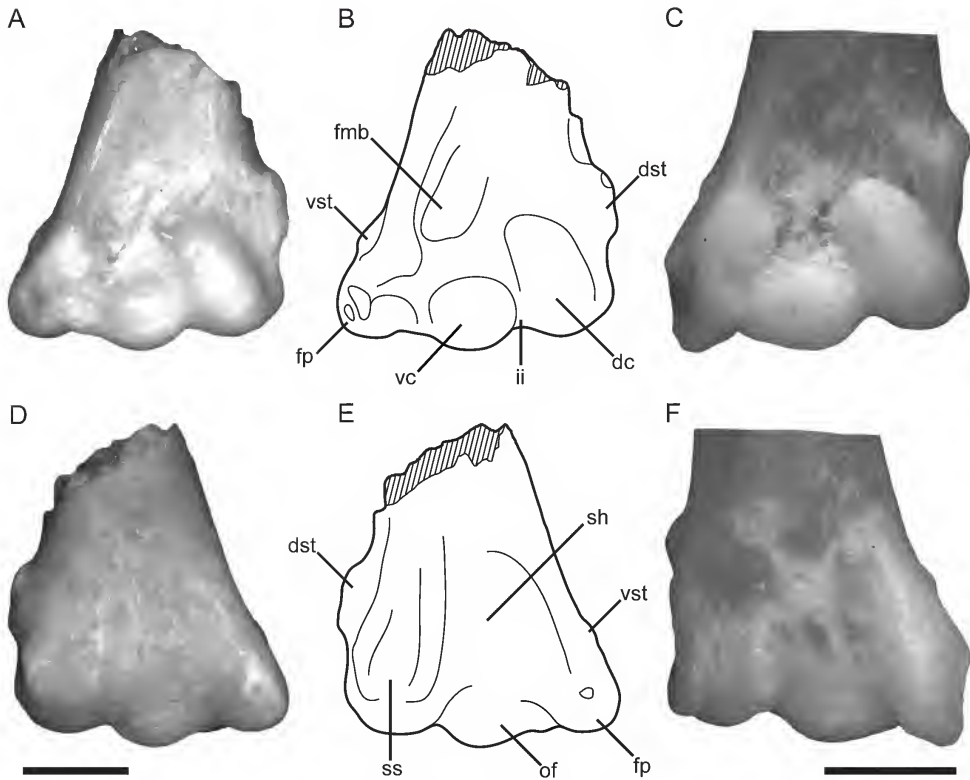


FIGURE 6. Photographs and interpretive line drawings of the Mongolian left distal humerus, IGM 100/1360, in **A**, **B**, cranial; and **D**, **E**, caudal views, and the left distal humerus of Sora Rail *Porzana carolina* (TMM M-10382) (Rallidae) in **C**, cranial; and **F**, caudal views. Abbreviations: **dc**, dorsal condyle; **dst**, dorsal supracondylar tubercle; **fp**, flexor process; **ii**, intercondylar incisure; **fmb**, fossa for the m. brachialis; **of**, olecranon fossa; **sh**, sulcus for the m. humerotricipitalis; **ss**, sulcus for the m. scapulotricipitalis; **vc**, ventral condyle; **vst**, ventral supracondylar tubercle. Scale bars = 2 mm.

Miocene *Palaeoramides* (Rallidae), and in the extant *Aramides saracura* (Rallidae) and *Podica senegalensis* (Heliornithidae) (Mayr, 2007; Mayr and Smith, 2002; Louchart et al., 2005). However, many of these characters are not apomorphic to the clade and are also seen outside this group. Therefore, while this new fossil may show affinities to a clade formed by messelornithids, rails, and finfoots (Mayr, 2004), we do not feel it can be assigned confidently at this time. For example, a weakly projected but elongate dorsal supracondylar tubercle with a concavity along the margin is found in the taxa listed above but is not found in all rails; in the Miocene *Baselrallus intermedius* and *Porzana carolina* the tubercle is entirely convex, and this feature shows variability in form throughout the clade (De Pietri and Mayr, 2014). An elongate, concave dorsal supracondylar tubercle is also present in the Sunbittern *Eurypyga helias* (Eurypygidae), and even in charadriiforms like *Burhinus* and members of the Alcidae (Mayr, 2007; Smith, 2014). Traits such as the development of the flexor process and the situation of the fossa for the m. brachialis are also variable.

DISCUSSION

The fossils we report here add between three and five new taxa to the known avifauna of the earliest Eocene Naranbulag Formation of Mongolia. The distal humerus and partial furcula from shorebirds are the oldest definitive records of Pan-Charadriiformes. These specimens were not found in association and may represent different species; however, they likely belonged to similarly sized individuals, and both bones most resemble those of small plovers (Charadriidae) and sandpipers (Scolopacidae). The previous earliest-known and confidently assigned member of the charadriiform lineage is from a slightly younger deposit of the Nanjemoy Formation in North America (53.6–52.8 Ma; Mayr, 2016). Like IGM 100/1360, this North American record is composed only of a distal humerus displaying characters similar to small extant plovers (Mayr, 2016). The previous oldest Asian charadriiform, *Jiliniornis huadianensis*, is from the middle Eocene of the Ukraine, and was tentatively placed in Charadriidae by Hou and Ericson (2002). Remains referred to “Graculavidae” were reported from the late Cretaceous–early Paleocene Navesink and Hornerstown Formations of New Jersey, by Olson and Parriss (1987) as a potential stem lineage of shorebirds. However, these remains lack apomorphic support for placement within Pan-Charadriiformes and may not represent members of crown-group birds (Norell and Clarke, 2001; Clarke and Norell, 2002; Mayr, 2009; Smith, 2015). Several fossil birds from the earliest Eocene of Europe have been described as “charadriiform-like” (e.g., *Vanolimicola longihallucis* from Germany: Mayr, 2017; *Scandiavis mikkelsenii* from Denmark: Bertelli et al., 2013), but have not been unambiguously referred to Pan-Charadriiformes. None of these European specimens preserve the pectoral girdle, so they cannot be directly compared to the humerus or furcula reported here. Without new material and phylogenetic analyses, whether the Bumban remains are crown- or stem-clade Charadriiformes cannot be assessed, hence our referral to Pan-Charadriiformes. No preserved morphologies exclude these remains from part of the crown clade.

The new quadrate would comprise the earliest-known worldwide record of the flamingo/grebe lineage, displacing *Juncitarsus* from slightly younger deposits in North America and Europe (Olson and Feduccia, 1980; Peters, 1987; Ericson, 1999). The faceted pterygoid articulation in IGM 100/1418 is markedly different from the projecting knob condition observed in both extant flamingos and grebes, possibly shedding light on the evolution of feeding style in both groups. In birds, the pterygoid articulation of the quadrate plays a crucial role in cranial kinesis, anchoring the pterygoid-palate complex so that forward motion of the quadrate results in an upward movement of the upper mandible relative to the braincase (e.g., Bout and Zweers, 2001, and references therein). Although the precise functional consequences of the difference in shape between IGM 100/1418 and living mirandornithines are unclear without more fossil material and new phylogenetic optimization of these traits, the morphology in the fossil is consistent with that observed in birds that feed by pecking on a hard substrate (Samejima and Otsuka, 1987; Gussekloo, 2005). This form is also seen in the stem flamingo *Palaelodus*, which exhibited a straight, blunt beak proposed to be adapted for pecking (Mayr, 2015), and in *Presbyornis*, which is proposed to have been only weakly adapted for filter feeding (Zelenkov and Stidham, 2018). By contrast, extant flamingos are highly specialized filter feeders, and grebes

exhibit a range of beak shapes adapted for crushing small crustaceans and catching fish. The apparent presence of a pecking-consistent morphology prior to the divergence of flamingos and grebes (the new quadrate), as well as early in the flamingo lineage (*Palaelodus*), may provide insight into the feeding ecology ancestral for Mirandornithes.

The fossils described here newly suggest that the shorebird and flamingo/grebe lineages were established in Asia by the beginning of the Eocene. Although the higher-order phylogenetic affinities of both groups remain controversial (Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015), the recent investigation of avian phylogenomics by Prum et al. (2015) recovered shorebirds and flamingos/grebes in a clade diverging in the middle Paleocene (~62–58 Ma). This divergence may have occurred in Asia, followed by dispersal of both groups across the rest of the northern hemisphere. However, further material is necessary to assess this hypothesis.

The additional material described here indicates other new taxa from the Bumban Member. The humerus, IGM 100/1360, is most like ralloids (rails and finfoots), and may represent a new gruiform record. While this new humerus cannot be confidently referred to any specific avian clade, it is not consistent with any previously described taxa from Asia and thus likely represents a new species record. The coracoid IGM 100/1371 is the second record of Pangalliformes from this locality. Though the humerus described by Hwang et al. (2010) likely came from a similarly sized individual to that of the new coracoid, a direct comparison cannot be made between these nonoverlapping elements.

These new fossils expand known species richness in Asia in the early Eocene. However, known taxonomic diversity remains relatively low compared to Europe and North America. Like the early Eocene Green River Formation of North America, the Bumbanian fossil record remains dominated by *Presbyornis mongoliensis* (Kurochkin and Dyke, 2010). The fossils reported here are consistent with the “transitional from fluvial to lacustrine” setting proposed for the Bumban Member exposure at Tsagaan Khushuu (Kondrashov, 2004:165), as shorebirds and stem flamingo-grebes, as well as the waterfowl *Presbyornis*, suggest the presence of standing water. Unambiguous presbyornithid remains are not known from Europe (e.g., Mayr, 2009), possibly indicating that the Bumbanian avifauna is more like North American than European faunas. Also like in North America, presbyornithid-like taxa at Naranbulag are known from both the late Cretaceous and the Paleogene (Kurochkin et al., 2002; Clarke and Norell, 2004; Kurochkin and Dyke, 2010), suggesting that this clade survived the K-Pg extinction event in both regions. Recovery of further avian material may inform a fuller reconstruction of both the paleoenvironment at this site and understanding Asian taxonomic diversity from the early Paleogene.

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